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Ecological implications of pedogenesis and geochemistry of ultramafic soils in Kinabalu Park (Malaysia)

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ABSTRACT

In Sabah, Malaysia, ultramafic rock outcrops are widespread (totalling 3500 km², one of the main outcrops in the tropical zone), and predominantly of the peridotite type. However, strongly serpentinised peridotite is also locally common, particularly along fault lines in the Mt. Kinabalu area. This study aimed to determine the extent of chemical variation in ultramafic soils in relation to the degree of serpentinisation and the weathering intensity, and consequent potential ecological implications linked to resulting soil chemical fertility. It was hypothesized that young soils and derived from bedrock with a significant degree of serpentinisation strongly differ from typical geric Ferralsols and result in soil chemistries with more adverse properties to plant life (*e.g.* low availability of the essential nutrients N, P, K and Ca and high concentrations of potentially phytotoxic Mg and Ni). Ultramafic soil diversity linked to the age of the soil or the degree of serpentinisation would thus be a main factor of plant diversity and distribution. The diverse topography of Kinabalu Park (ultramafic soils present between 400–2950 m asl) has given rise to high pedodiversity with the broad overall ultramafic soil types being: (i) deep laterite soils (Geric Ferralsols); (ii) moderately deep montane soils (Dystric Cambisols) with mor humus; (iii) shallow

35 skeletal soils at high altitude (Eutric Cambisols Hypermagnesian); and (iv) bare serpentinite soils
36 (Hypereutric Leptosols Hypermagnesian) at low altitude (200–700 m asl). Leptosols on serpentinite
37 and Eutric Cambisols have the most extreme chemical properties in the whole Kinabalu Park area
38 both with very high Mg:Ca molar quotients, with either high available Ni (Cambisols) or high pH
39 (Leptosols). These soils host specific and adapted vegetation (high level of endemism) that tolerates
40 geochemical peculiarities, including Ni hyperaccumulators. Geric Ferralsol present far less
41 chemical constraints than hypermagnesian serpentine soils to the vegetation and host a tall and very
42 diverse rainforest, not so different than that on non-ultramafic soils. It therefore appears that
43 altitude, soil age and degree of bedrock serpentinisation are the main determining factors of soil
44 properties: the qualifier “ultramafic” alone is not sufficient to define soil geochemical and
45 ecological conditions in the Kinabalu Park area, probably more than in any other ultramafic region
46 in the world.

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48 **Keywords:** *hypermagnesian soils; laterite, Mg:Ca quotient, phytotoxicity, serpentinisation,*
49 *pedodiversity.*

50

1. INTRODUCTION

1.1 Properties of ultramafic soils

Ultramafic bedrock is part of the upper mantle (peridotite) obducted in continental margins (Searle and Stevens, 1984). Such outcrops are widespread but relatively rare, covering >3 % of the surface of the earth (Guillot and Hattori, 2013). The largest ultramafic regions in the world can be found in temperate (e.g. Balkans, Turkey, California) and in tropical environments (e.g. New Caledonia, Cuba, Brazil, Malaysia, Indonesia). Southeast Asia probably has the largest tropical outcrops in the world with Borneo and Sulawesi totalling over 23 000 km² (Van der Ent et al. 2013). The rock-type peridotite is made up from magnesium-iron-silicates in the minerals olivine and (ortho)pyroxene (Coleman, 1971). Low-temperature hydration and metamorphism of peridotite leads to serpentinite, usually at the sea floor along tectonic boundaries (such as near mid-ocean ridges) or during continental emplacement (Lewis et al. 2006; Guillot and Hattori, 2013). During serpentinization, the mineral assemblage is completely altered to metamorphic equivalents, and only chromite usually remains unaltered (Coleman 1971; Alexander, 2009). Serpentinite rocks contain very high Mg (18–24%) and high Fe (6–9%) but very low Ca (1–4%) and Al (1–2%) concentrations (Alexander, 2004). The total transformation of peridotite to serpentinite needs 14% water and the rock expands by 33% from dense peridotite (3.2–3.3 g cm³) to less dense serpentinite (2.4–2.6 g cm³) (Alexander, 2009). This results in fracturing and shearing of the rock, and makes many serpentinite outcrops prone to landslides. As such, the weathering properties of serpentinite rocks are dramatically different from peridotite bedrock. All near-surface ultramafic rock is serpentinised to varying degrees, and serpentinite is used to describe rocks containing >50% serpentine-group minerals (*i.e.* antigorite, chrysotile, lizardite) in which the original (primary, or not metamorphosed) mineralogy is obscured (following Jacobson, 1970). Ultramafic rock generally itself only contains 0.16–0.4% nickel (Butt, 2007) however these initial concentrations increase significantly during surface weathering in humid tropical climates, resulting over the long term, in nickel laterite soils (Echevarria, 2017). Such nickel-enriched ultramafic soils are a major target for nickel and cobalt mining industries, particularly in tropical settings such as in Cuba (Roqué-Rosell et al. 2010), Brazil (Colin et al. 1991), Indonesia, the Philippines and New Caledonia (Butt, 2007; Fan & Gerson 2011).

Properties commonly shared among ultramafic soils include high iron (Fe) and magnesium (Mg) concentrations and low Aluminium (Al) concentrations, relatively high concentrations of chromium (Cr), cobalt (Co) and nickel (Ni), high magnesium-to-calcium (Mg:Ca) quotients in the exchange complex and low concentrations of phosphorus (P) and potassium (K) (both total and extractable).

86 In ultramafic laterites (*i.e.* Ferralsols), some of these features might be less strongly marked because
87 intense weathering has erased the fingerprint of geochemical peculiarities: *i.e.* a higher Aluminium
88 (Al) concentrations and a much lower magnesium-to-calcium (Mg:Ca) quotients than in ultramafic
89 Cambisols or Luvisols (Echevarria, 2017).

90

91 **1.2 Geology of ultramafic outcrops in Kinabalu Park**

92 Ultramafic outcrops cover 3500 km² in Sabah (Proctor et al. 1988; Repin 1998) and 151 km² in
93 Kinabalu Park. The ultramafic rocks are part of an ophiolite suite which derived from a collision
94 suture between the Kalimantan micro-continent and the Sulu Arc (Imai and Ozowa, 1991) when
95 oceanic lithosphere of the Sulu Sea was obducted (McManus and Tate, 1986). Mount Kinabalu
96 (4095 m) is a granite intrusion dated 7.2 to 7.9 Ma before present (Cottam et al., 2010) and
97 ultramafic outcrops form a ‘collar-like’ distribution on the mid-elevation around the Kinabalu
98 granite core. In the northern part of Kinabalu Park lies Mount Tambuyukon (2579 m). Of the
99 outcrops in Kinabalu Park, Mount Tambuyukon is the largest (89 km²), but many small outcrops
100 (<1 km²) also exist. In the Kinabalu area the most common peridotite is Iherzolite, and tremolite-
101 bearing peridotites whereas harzburgite and wehrlite are rare (Jacobson, 1970).

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103 **1.3 Pedogenesis and mineralogy of ultramafic soils**

104 Ultramafic bedrock contains on average approximately 0.2% Ni, 0.02% Co, 10% Fe and 0.2% Cr
105 (Butt and Cluzel, 2013). A recent article summarises the main factors involved in ultramafic
106 pedogenesis (Echevarria, 2017). In tropical settings, weathering of ultramafic bedrock leads first to
107 secondary phyllosilicates (Cambisols), then to amorphous and poorly-crystalline Fe-Cr-Mn oxides,
108 and finally to crystalline Fe-oxides (Schwertmann and Latham, 1986; Becquer et al., 2006;
109 Echevarria, 2017). On well-drained soils, peridotite minerals (olivine and pyroxenes) weather to
110 form secondary (Fe-rich) minerals (goethite, hematite), and Mg and Si move down the soil profile
111 and accumulate at depth (Latham, 1975b; Trescases, 1975; Proctor, 2003) whereas Fe, Cr and Al
112 are less soluble and remain higher up in the profile. Ni is also highly leached during pedogenesis
113 and most of it is lost in contrast to other metals, e.g. Al (Estrade et al., 2015; Echevarria, 2017). The
114 results are deep red laterite soils consisting of a limonite (Fe-oxide) layer and a saprolite (Mg, Si-
115 rich) layer (Gleeson et al., 2003). Total Cr concentrations are generally very high in the limonite
116 layer. The secondary Fe and Mn oxides are known to be a major sink for Ni because of their high
117 sorption capacity (Becquer et al. 2001), often containing 0.8–1.5 wt.% Ni (Fan and Gerson, 2011).
118 The Ni, Mg and Si leached into the saprolite are the main ‘ore’ mined in the lateritic nickel mining
119 industry, where Ni is embedded in phyllosilicate minerals (Freyssinet et al., 2005) as a substitution
120 for Mg. This layer can contain up to 5 wt.% Ni, and in garnierite over 20 wt.% Ni (Fan and Gerson

2011), but the average is 2–3 wt.% (Elias, 2001). The nature of secondary phyllosilicates in saprolites varies according to the composition of the peridotite (total Si content) from serpentine minerals to Fe-rich smectites (Raous et al., 2013). Well-drained profiles can be 20 m deep in the Philippines (Fan and Gerson 2011) and New Caledonia (Latham 1975b; Dublet et al. 2012) or more such as in Niquelândia, Brazil (Colin et al. 1990), but are usually <5 m in Sabah. These regoliths are termed nickel laterites (Butt and Cluzel 2013), ‘*sols ferralitiques ferritiques*’, or Geric Ferralsols (Latham 1975b; Becquer et al. 2006). Ferralsols can occur on serpentinite which produces a smectite-rich saprolite material such as for pyroxenite (Echevarria, 2017). Due to the high susceptibility of erosion that can affect smectite-rich saprolites, Ferralsols on serpentinite are seldom observed because they are easily truncated (Echevarria 2017); such laterites, when reported, are usually extremely old and occur in flat landscape positions (Youngué-Fouateu et al. 2007). Ferralsols soils can also form in the montane zone on steeper slopes, but these soils are much shallower and do not feature an extensive limonitic layer and often have (in the upper montane zone) significant build-up of organic matter (mor-type humus). In the New Caledonian context these soils are termed ‘*sols à accumulation humifère*’ (Latham 1975; 1980) or ‘Inceptisols’ (tropepts) in the USDA classification (Burnham, 1975; Bruijnzeel et al. 1993). Between the two extremes many varieties exists as a result of local erosion, colluvium and climate (Jaffré, 1992). At high altitude, very shallow skeletal soils (Cambisols) form, which are a direct product of primary weathering of the bedrock close to the surface. Excess Si recrystallizes to form quartz and chalcedony and excess Mg reacts with atmospheric carbon dioxide and precipitates as magnesite (Proctor 2003). These soils (‘Eutric Cambisols Hypermagnesianic’ ‘*sols bruns eutrophes hypermagnésiens*’ viz. Jaffré and Latham 1974; Latham 1975a; Jaffré 1980; or ‘Hypermagnesianic Hypereutric Cambisols’ viz. Chardot et al. 2007) have extremely high Mg:Ca quotients as well as high available Ni as a result of the disintegration of phyllosilicates and re-sorption onto secondary Fe-oxides or high-charge clays (Bani et al. 2014; Estrade et al. 2015; Echevarria 2017).

Coleman and Jove (1992) empathised the importance of distinguishing between the weathering of peridotite, and serpentinite derived from peridotite, the first being mineralogically extremely unstable and the latter relative stable. Serpentine mineral dissolution under surface conditions is a rather low process compared to the dissolution of olivines or pyroxenes (Chardot-Jacques et al. 2013). More recently, a study showed how peridotites and serpentinites influence soil composition and metal geochemistry in a different way under temperate conditions (Kierczak et al. 2016). The mineral composition of azonal serpentinite soils (*i.e.* soils derived from disintegrated serpentinite colluvium, probably Cambisols) therefore contains both primary minerals (chrysotile, antigorite, lizardite) and secondary minerals (smectites, magnetite, chlorite, talc) (Chardot et al. 2007; Bani et

al. 2014). Generally, Ferralsols and Dystric Cambisols are oligotrophic with very low base saturation and very low and low CEC respectively, whereas hypermagnesian Cambisols and serpentinitic Leptosols are eutrophic (sometimes dystrophic) with high base saturation and CEC (Echevarria, 2017). Ferralsols, as per their definition, have no weatherable minerals in the ferralic horizon. Cambisols have a Bw (weathering) diagnostic horizon where weatherable minerals are significant in proportion, which includes high activity clays resulting in a high CEC ($>24 \text{ cmol kg}^{-1}$). ‘Montane inceptisols’ are classified as Cambisols in the WRB, but have strong connections with the specific group of Ferralsol (they have most of the ferralic properties except the depth development).

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166 **1.4 Trace element speciation and toxicity in ultramafic soils**

Although nutrient limitations and cation imbalances have been frequently studied as a cause of the disjunct vegetation on temperate ultramafic soils (Walker et al. 1955; Proctor 1970; Nagy and Proctor 1997), relatively high total concentrations of the trace elements Ni, Cr and Co in ultramafic soils have also been linked to potential phytotoxic effects (Brooks 1987; Proctor 2003). However, in humid tropical conditions, the most important factor in controlling ultramafic vegetation development seems to be soil depth (Proctor et al. 1999). The potential effects of Ni, Cr, Co and Mn toxicities on native vegetation as a whole are largely unknown, however, despite clear evidence of toxicity of these elements to plants in experimental work (Anderson et al. 1973; Taylor et al. 1991; L’Huillier et al. 1996). Nickel, in particular, has been attributed as one of the main causes for the stunting of some types of ultramafic vegetation (Brooks, 1987, Brady et al. 2005), but it is probable that other geochemical factors such as low nutrient (i.e. K and P) levels – or combinations of Ni stress and low K and P – also play a role in these phenomena (Proctor 2003). The phytotoxicity of Ni depends mainly on soil-specific chemistry, in particular the mineralogy of Ni-bearing phases (high-exchange clays and poorly-ordered hydrous Fe and Mn oxides contain available forms) and soil acidity (pH decreases Ni adsorption to release phytotoxic Ni ions) (Hunter and Vergnano 1952; Crooke 1956; Halstead 1968; Echevarria 2017). In laterite soils, Ni is predominantly associated with crystallised Fe-oxides (such as goethite) and Mn-oxides (such as birnessite and lithiophorite), whereas in serpentinite soils, Ni is predominantly associated with phyllosilicates and smectite clay minerals when they form (Lee et al. 2003; Massoura et al. 2006; Fan and Gerson 2011; Dublet et al. 2012; Bani et al. 2014). Despite very high total concentrations, extractable/phytoavailable concentrations of chromium are generally extremely low as soil Cr-bearing minerals (such as chromite, Cr-magnetite) weather extremely slowly (Oze et al. 2004; Garnier et al. 2006). However, Cr-VI pools in such soils can reach high concentrations (approx. 0.1 wt%) and they are often highly available (Garnier et al. 2009). Although Co is relatively more soluble in ultramafic soils compared

to Cr, it is present at much lower total concentrations than either that metal or Ni, and its fate is specifically associated with that of Mn. Also, very little is known about any (toxic) effects Co might have on plants growing in tropical ultramafic soils.

1.5 Ultramafic ecosystems in Kinabalu Park

Kinabalu Park is renowned for its plant diversity with over 5000 recorded plant species (Beaman, 2005), partly the result of its variety of soils derived from a range of very contrasted bedrock types ('geodiversity'). Chemical characterization of ultramafic soils is important for understanding the ecology and plant/soil interactions of these ecosystems and the specific role played by intrinsic ultramafic rock diversity in the overall species richness and diversity of Kinabalu Park. Although the distinctiveness of ultramafic soils compared to non-ultramafic soils is often emphasized (Brooks 1987), it is not generally acknowledged that ultramafic soils themselves vary greatly in chemical characteristics, and important differences between plant community compositions on different ultramafic soils, at the same altitude, have also been observed (Borhidi 2004). Although the term serpentine is frequently used to describe ultramafic geology, this is incorrect, as serpentine group minerals are only a subset of those associated with ultramafic rocks (Brooks 1987; Brady et al. 2005). Nickel hyperaccumulator plants in Sabah were found to occur exclusively on young soils that were found on strongly serpentinised bedrock (van der Ent et al. 2015; van der Ent et al. 2016a).

This study aimed to determine precisely the extent of chemical variation in ultramafic soils in relation to the level of serpentinisation and weathering intensity, and consequent potential ecological implications linked to soil chemical fertility. Firstly, the objective was to compare ultramafic soil geochemistry to adjacent non-ultramafic soils to verify the existence of a geochemical shift on this substrate. Secondly, it was hypothesized that soils young soils on peridotite with low amounts of serpentine minerals and all soils derived from serpentinite (i.e. containing more than 50% serpentine minerals after Jacobson 1970) bedrocks (i.e. serpentinite vs. peridotite) result in soil geochemistry with more adverse properties to plant life, which in turn results in more adverse geochemical properties to plant life (e.g. low availability of essential nutrients and high concentrations of potentially phytotoxic Mg, Cr and Ni). In total, 87 non-permanent vegetation plots were established covering all major 12 'ultramafic edaphic islands' known in Kinabalu Park. In each 'island', at least four plots were laid out, with plot sizes determined by altitude. The altitude ranged from 474 to 2950 m above sea level (asl).

2. MATERIALS AND METHODS

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2.1 Site survey and sample collection

Figure 1 shows the overall geology and main ultramafic outcrops in the study area. Soil profiles were observed and soil and bedrock samples were collected from 13 different ultramafic sites in Kinabalu Park, within an area of approximately 700 km² as part of an ecological study (for details refer to Van der Ent et al. 2016b). The objective in the sampling was to account for the geological variability within ultramafic rocks (from non-serpentinised peridotite, including dunite, to serpentinite) as well as for edaphic and vegetation variability. Therefore, bedrock samples were carefully observed during the field survey to determine if they were from the serpentinite type or the non- or poorly-serpentinised peridotite type. For some of them, further X-ray diffraction mineralogy was used to confirm the observations and the local available descriptions of ultramafic rock outcrops (Jackson 1970; Imai & Ozawa 1991; Tashakor et al. 2017). In particular, the degree of serpentinisation of peridotites is well documented in the areas of Mt. Kinabalu and Ranau (Jacobson 1970; Tashakor et al. 2017). Areas of Mt. Tambuyukon and the Serinsim lateritic plateau are much less documented (van der Ent et al. 2016a). Table 1 reports relevant site attributes (altitude, slope, bedrock type, soil type, soil depth, vegetation) and the number of samples collected from each site. At each site, at least three soil samples (1–2 kg) and one bedrock sample (2–3 kg) were collected. Each soil sample was collected in the A₁ horizon, and care was taken not to include organic constituents in surface layers. The bedrock samples were collected from a soil pit at each site. The sites ranged in elevation from 474 to 2950 m and included a total of 95 discrete sample localities (dispersed within each ultramafic site). In addition to the shallow soil samples, five soil profiles were also excavated and samples were collected from all horizons down to the bedrock. Non-ultramafic soil and bedrock samples were collected from Kinabalu Park, near park headquarters (1550 m), around Layang-Layang (2700 m) and from nearby Mount Trus Madi (1600–2450 m) to serve as a comparison dataset to contrast the ultramafic soils and bedrock. The underlying bedrock from the non-ultramafic soils was sandstone, shale and granite. Soil profiles were described at a 36 m deep profile near Hampuan on strongly serpentinised peridotite (i), a 22 m deep profile at Sunsui with a full limonite to saprolite layering (ii), a 0.9 m deep profile in lateritic (Ferralsol) regolith near Serinsim (iii), and two profiles in serpentinitic Leptosols, 0.75 m and 0.9 m deep, respectively, near Wuluh River (iv and v). All soil samples were packed, brought to the local field station, air-dried at room temperature to constant weight (3–4 weeks), sieved to <2 mm, shipped to Australia, and gamma irradiated at Steritech Pty. Ltd. in Brisbane following Australian Quarantine Regulations. The rock samples were treated identically to the soils, but were dried in an oven at 70°C for 48 hours and ball-milled and sieved to <100 µm fraction.

2.2 Laboratory analyses: soil chemistry

The analysis of the soil samples took place at the laboratory of the Centre for Mined Land Rehabilitation (CMLR) at The University of Queensland in Australia. The soil samples (300 mg) were digested using freshly prepared Aqua Regia (9 mL 70% nitric acid and 3 mL 37% hydrochloric acid per sample) in a microwave for a 1.5-hour programme and diluted to 45 mL with ultrapure (TDI) water before analysis. The method was based on Rayment and Higginson (1992) method 17B2. This method yields 'pseudo-total' elemental concentrations in soil matrices (*viz.* Rayment and Higginson, 1992). Soil pH and electrical conductivity (EC) were obtained in a 1:2.5 soil:water mixture. Plant-available phosphorus ('ML-3') was extracted with Mehlich-3 solution consisting of (0.2 M CH₃COOH + 0.25 M NH₄NO₃ + 0.015 M NH₄F + 0.013 M HNO₃ + 0.001 M EDTA at pH 2.50 ± 0.05) according to Mehlich (1984). Labile ('lab.') Ni, Co, Cr and Mn were extracted in 0.1 M Sr(NO₃)₂ at a soil : solution ratio of 1:4 (10 g : 40 mL) and 2 hours' shaking time (adapted from Kukier and Chaney, 2001). As a means of estimating potentially plant-available trace elements, DTPA-Ni, Co, Cr and Mn were extracted with Diethylene triamine pentaacetic acid (DTPA) according to Becquer et al. (1995), which was adapted from the original method by Lindsay and Norvell (1978), by the following modifications: excluding TEA, adjusted at pH 5.3, here an extraction time of 2 hours was used (instead of 1 hour) and a soil:solution ratio of 1:4 as Kukier and Chaney (2001) have demonstrated that the DTPA can be oversaturated with Ni in Ni-rich soils. A second method (loosely based on Feng et al. 2005) for extracting phytoavailable ('CA') Ni, Co, Cr and Mn was also employed, and used carboxylic acids (acetic, malic and citrate acid in molar ratio of 1:2:2 at 0.01 M) at a soil : solution ratio of 1:4 (10 g : 40 mL) and 2 hours shaking time. Exchangeable cations ('exch.') were extracted with silver-thiourea (Dohrmann, 2006) over 16 hours.

Ni, Co and Cr partitioning was evaluated with a 5-step selective sequential extraction scheme to provide operationally defined solid-phase trace element (Ni, Cr, Co, Mn) fractionation. This scheme is based on Quantin et al. (2002), which was in turn modified mainly from Leleyter and Probst (1999). Adaptations were made here by combining step 1 and step 2, and by using HNO₃/HF high-pressure microwave digests for the residual fraction (step 5) instead of an alkaline fusion as in Quantin et al. (2002). The step for the 'organic bound phase' was also omitted because the tested soils are extremely low in organic matter. As such the fractions were: water soluble and exchangeable (i), bound to Mn oxides (ii), bound to amorphous Fe oxides (iii), bound to crystalline Fe oxides (iv), and residual (v). After each extraction step, the tubes were centrifuged for 10 minutes at 4000 rpm and the supernatants were then filtered through 0.45 µm membranes.

296 The residues were washed with 20 mL of TDI water, centrifuged again for 10 minutes at 4000 rpm,
297 the water decanted, and the residue dried at 40°C prior to the next extraction step. All soil
298 extractions were undertaken in 50 mL polypropylene (PP) centrifuge tubes. Soil samples were
299 weighed using a 4-decimal balance. Samples were agitated for method-specific times using an end-
300 over-end shaker at 400 rpm, centrifuged (10 minutes at 4000 rpm) and the supernatant collected in
301 10 mL PP tubes. All soil samples were analysed with ICP-AES (Varian Vista Pro II) for Ni, Co, Cu,
302 Zn, Mn, Fe, Mg, Ca, Na, K, S and P. Each method included three sample blanks, two NIST
303 standards, two ASPAC reference soils, three random sample duplicates and three multi-element
304 standards as part of the quality control. The ICP-AES instrument was calibrated using a 6-point
305 multi-element standard (Ni, Cu, Fe, Mg, Ca, K) prepared in each extraction solution.

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307 Total elemental concentrations in rock samples (100 mg) were obtained by digestion with a mix of
308 4 mL 70% nitric acid, 3 mL 37% hydrochloric acid and 2 mL 32% hydrofluoric acid per sample in
309 a microwave for a 2-hour programme and diluted to 45 mL before analysis. The method was based
310 on Rayment and Higginson (1992) method 17A2. The aliquots were also analysed with ICP-AES as
311 detailed above.

312

313 **2.4 Laboratory analyses: soil and rock mineralogy**

314 Bedrock and soil samples were analysed for mineral constituents at the University of Rhode Island,
315 Department of Geosciences (Kingston, RI). Samples were individually powdered using percussion
316 mortar and manual mortar and pestle, and passed through a 150-micron sieve. X-ray diffraction
317 (XRD) profiles were collected with an Olympus (formerly InXitu) Terra Mobile XRD System, a
318 field portable unit with extremely robust performance (Blake et al., 2012). The Terra is outfitted
319 with a micro-focus X-ray tube (nominal operating voltage of 28 keV, filament current of 1.5 A,
320 cathode output of 100 μ A) with a Co anode, which yields continuum and characteristic X-radiation
321 from a 50 μ m diameter spot on the Co anode (Blake et al., 2012). 250 exposures generate a well-
322 defined diffractogram for comparison with reference data files. Minerals were thus detected in the
323 complex natural mixtures by comparing sample diffractograms with known reference
324 diffractograms for individual minerals. Similarly, mineral phases were detected in soil samples
325 from the profiles with a Bruker D8 Advance X-Ray diffractometer (at the University of
326 Queensland, Australia) equipped with a copper target, diffracted-beam monochromator, and
327 scintillation counter detector. Conditions for running the samples were: 40 kv, 30 mA, 3-80° 2 θ ,
328 0.05° step size or increment, with 10 seconds per step.

329

330 Using the commercially available XRD peak analysis software, X Powder (available at
331 <http://www.xpowder.com/>), relative abundances of component minerals in rocks and soils were
332 modelled as mixtures of 8 reference minerals common to ultramafic rocks using a reference
333 intensity ratio approach. The samples studied here were considered mixtures of the following
334 minerals: diopside (a pyroxene, PDF 016581), tremolite (an actinolite-type amphibole, PDF
335 011983), antigorite (a serpentine variety, PDF 018242), lizardite (a low temperature serpentine
336 variety, PDF 015238), forsterite (Mg-rich olivine, PDF 023357), spinels (representing spinel group
337 minerals including magnetite, PDF 018254), talc (PDF 019690) and montmorillonite (a smectitic
338 clay mineral, PDF 012866). Modelled proportions of these minerals should be considered estimates,
339 given for example that spinel and magnetite are binned under “spinel,” multiple clay minerals
340 share the 14 to 16 Å peak characteristic of smectite group clays, *etc.* Given that the same modelling
341 strategy was applied across all samples, relative differences in major minerals can be observed in
342 the results. Of course, modelling only provides an incomplete description of the mineralogy and
343 should be taken with much caution.

344

345 **2.5 Statistical analysis**

346 The soil and rock chemistry data was analysed using the software package STATISTICA Version
347 9.0 (StatSoft), Excel for Mac version 2011 (Microsoft) and PRIMER Version 6 (PRIMER-E). The
348 XRD data was analysed with the X Powder software program (version 1.0), and with DIFFRACplus
349 Evaluation Search/Match Version 8.0 and the International Centre for Diffraction Data’s PDF-
350 4/Minerals database. The map was prepared in ArcGIS version 10 using geological database files
351 prepared by Robert Hall (Royal Holloway University, London). Non-metric multidimensional
352 scaling (NMDS) are undoubtedly the most widely accepted and routinely used ordination technique
353 for soil and plant data. NMDS of pseudo-total soil elements (A) and exchangeable and extractable
354 elements (B) from all collection sites, contrasted with non-ultramafic comparison soils was carried
355 out. The 4 main soil types found in the areas investigated were nominally outlined in the NMDS-
356 plots (based on site typology, see Table 1).

357

358 **3. RESULTS**

359

360 **3.1 Bedrock elemental chemistry and mineralogy**

361 Summarized chemistry of ultramafic bedrock samples (n = 76) is given in Table 2. These analyses
362 are compared with samples from non-ultramafic bedrock from Kinabalu Park and nearby Mount
363 Trus Madi (n = 13). Mean concentrations of Ca, Co, Cr, Cu, Fe, Mg, Mn, Ni and Zn are all
364 markedly higher in ultramafic rock than in non-ultramafic rock samples, whereas K, Na, P and Si

are higher in non-ultramafic rock. Compared to the protolith initial concentrations, the elements Al, Ca, Mg, Co, Ni and Zn are significantly enriched during weathering and soil formation.

X-ray Diffraction analyses of rock samples show that minerals such as olivines (forsterite), pyroxenes (diopside, enstatite), amphibole, and spinels (chromite, magnetite) characterize the mineralogy of the peridotite bedrock (Figure 2). All ultramafic rocks present in the Kinabalu Park area are serpentinised to varying degrees, however, the more serpentinised samples also contain talc, chlorite, and magnetite as minerals in addition to serpentines, olivines and pyroxenes.

3.2 Soil elemental chemistry

Table 3 presents summarised bulk chemistry of ultramafic soils, contrasted with non-ultramafic soils. Mean pseudo-total concentrations of Al and P were roughly similar among soils, whereas concentrations of Ca, Co, Cr, Fe, Mg, Mn and Ni were unsurprisingly much higher in ultramafic soils. On the other hand, pseudo-total concentrations of K were higher in non-ultramafic soils. The mean DTPA-extractable trace elements (Co, Cr, Cu, Ni and Zn) were all higher in ultramafic soils, except for Fe, which is similar. Potentially plant-available P (Mehlich-3 extract) was more than four times higher in average in non-ultramafic soils than in ultramafic soils (mean 12 vs. 2.7 $\mu\text{g g}^{-1}$). The soil pH range was 3.5 to 9.7 for all soils. Generally, the ultramafic soils were less acidic than the non-ultramafic soils with a mean pH of 6.0 as opposed to the much lower value of 4.6 for non-ultramafic soils. However, there was a wider range of pH values among ultramafic soils than among non-ultramafic soils: ultramafic laterites display acidic pH values as on non-ultramafic substrates whereas soils on serpentinite have unusually high pH values, see Table 4). Mean exchangeable Ca, Mg and Na were much higher in ultramafic soils, and exchangeable K was similar between ultramafic and non-ultramafic soils (Table 3). Mean exchangeable Al was much higher in non-ultramafic soils. The Mg:Ca in the exchangeable complex was always <1 in non-ultramafic soils (mean is 0.2) and > 1 (mean is 5.3) in ultramafic soils. Exchangeable K was very low and exchangeable Mg was relatively high, and the Mg:Ca molar quotient in some soils is extremely high (up to 82). Consequently, the electrical conductivity (EC) was also higher in ultramafic soils than in non-ultramafic soils. Soil pseudo-total elements of the main ‘ultramafic edaphic islands’ are shown in Table 4, whereas soil extractable trace elements, exchangeable macro-elements are shown in Table 5.

3.3 Soil mineralogy and pedological markers in selected profiles

Among soils, we observed several features of mineralogy and pedogenic indices of selected profiles (Figures 2 & 3, Table 6 & 7). Firstly, Hypereutric Leptosols displayed horizons that were highly

serpentine-rich, with a limited smectite component, and also contained primary magnetite. In Eutric Cambisols (Hypermagnesian), some of the primary minerals were still substantially present in the Bw horizons. In these soils (e.g. Cambisol at Tambuyukon summit), we observed a mixture of primary silicate minerals (amphiboles, pyroxenes and talc) and secondary Fe oxihydroxides (goethite). In more developed Geric Ferralsols, no trace of primary minerals could be found except spinels (i.e. magnetite and chromite). The mineralogy of B lateritic horizons (i.e. ferralic horizon) was dominated by goethite (e.g. Serinsim). Pisolithes can be found at the surface of such soil profiles that usually derived from crystallisation and dehydration of oxihydroxides. General features of all soil profiles but Leptosols included relatively acidic surface horizons with a marked increase in soil pH and in Mg:Ca ratios with a depth (Table 8). This rise in pH (and CEC) coincides with the increase in exchangeable Mg and Ca ions. Along with pH and CEC saturation increase was the increase of the Mg:Ca ratio with depth. Calcium was better retained by the CEC than Mg in A and B horizons of Ferralsols. In the hypermagnesian Leptosols, no such differentiation was observed and surface CEC was saturated by Mg.

3.4 Metal bearing-phases and availability in soils

The sequential extraction (Figure 4) showed that amorphous Fe-oxides ('AM-Fe') were important phases for Ni and Cr in Eutric and Dystric Cambisols, but not in Geric Ferralsols where crystalline Fe-oxides ('CR-Fe') were by far the dominating fraction of Fe-oxides. In all soils, exchangeable Cr was extremely low (not visible on the graph), whereas exchangeable Ni in Hypereutric and Dystric Cambisols was relatively high (up to several % of total Ni). In contrast, exchangeable Co was extremely high in some Geric Ferralsols, but not in Hypereutric Leptosols. Residual concentrations for all four elements made up >50% of the total partitioning although many studies report incomplete dissolution of crystalline Fe-oxides with one single DCB extraction (Becquer et al., 2006).

The carbolic acid extractable Co was extremely high in the Eutric Cambisols Hypermagnesian with up to 122–263 $\mu\text{g g}^{-1}$ (on Mount Tambuyukon), whereas extremely high extractable Ni occurred in both Eutric Cambisols Hypermagnesian on Mount Tambuyukon (176–404 $\mu\text{g g}^{-1}$) and in Leptosols (Hypermagnesian) at Wuluh River (240–414 $\mu\text{g g}^{-1}$). Pseudo-total Mn concentrations were highest in Dystric Cambisols and Cambisols (Hypermagnesian) in the high-altitude zone of Mount Tambuyukon, reaching up to 33 590 $\mu\text{g g}^{-1}$, probably because of humid conditions prevailing in these soils (due to the altitude). The carboxylic acid extractable Mn was also extremely high in these soils (up to 3727 $\mu\text{g g}^{-1}$). Likewise, pseudo-total and carboxylic acid extractable Ni were similarly extremely high (up to 7000 $\mu\text{g g}^{-1}$ and 404 $\mu\text{g g}^{-1}$ respectively) at this location and likely to

contribute to the toxicity of these soils. High pseudo-total Cu occurred on a variety of soils reaching up to 453 $\mu\text{g g}^{-1}$, but extractable concentrations were low in all soils.

3.5 Soil discrimination according to geochemical properties

Figure 5 shows two NMDS-plots of pseudo-total elements (A) and exchangeable and extractable elements (B) with the 13 different sites coloured-coded (and non-ultramafic comparison soils included). In the NMDS (Figure 5), the two major sets of opposing vectors were Mg, Na, Ca and Fe, Cr, with the Hypereutric Leptosols (4) clustering along the first, and the Geric Ferralsols (1) clustering along the far end of the second. The (Hyper)Eutric Cambisols (3) spread towards the Fe, Cr vector, and the Dystric Cambisols (2) were intermediate. The non-ultramafic comparison soils clustered towards the K and Al vectors, probably because of the scarcity of these two elements in ultramafic soils. The NMDS with extractable and exchangeable elements was very different, and only the Eutric Cambisols were immediately apparent towards the exchangeable Mg, Ca vector. The Eutric Cambisols clustered towards the carboxylic acid extractable Fe, Mn, Ni vector. The Dystric Cambisols were intermediate, whereas the Ferralsols clustered in the centre, which can be explained by extremely low extractable/exchangeable elements as a result of intensive leaching. The soils from Marai Parai are waterlogged and have extremely high exchangeable Al, similar to many of the sandstone-derived non-ultramafic soils. The soils from Bukit Hampuan, Bambang and Mesilau, all localities with complex geologies that contain serpentinite bedrock, evident in bedrock analysis and in the vegetation, cluster towards the exchangeable Mg, Ca vector.

4. DISCUSSION

4.1 Characteristics and distribution of the main ultramafic soil types

The characteristics of the (Hyper)Eutric Cambisols (Hypermagnesian) with extremely high Mg:Ca molar quotients and very high extractable Ni and Mn concentrations results from direct and moderate weathering of the bedrock with still many primary minerals, and hence the soil chemistry is largely a reflection of that bedrock. These soils are very shallow and boulders of bedrock dominate the surface with limited signs of soil formation processes, although mineral weathering shows evident signs of the formation of a Cambic horizon with a stable complex. Also, Ni release through mineral dissolution and its uptake by neo-formed high CEC clays and poorly crystallised Fe oxides, are favourable to its high availability (Massoura et al., 2006; Chardot et al., 2007; Echevarria, 2017). In these soils, Mg:Ca can be as high as 70, which is strongly unbalanced to ensure ideal plant nutrition. They are mainly found at Layang-Layang (high-altitude Mount Kinabalu) and in the summit zone of Mount Tambuyukon. These shallow soils present multiple

toxicities; extremely high phytoavailable Ni, Co and Mn and extremely high exchangeable Mg (and high Mg:Ca quotients) that are quite similar to those found in the ultramafic soils of the temperate and Mediterranean regions (Chardot et al., 2007; Bani et al., 2014) but also in ultramafic Eutric Cambisols from tropical regions (Borhidi 1988; Proctor 2003). In such peculiar geochemical conditions (or geochemical stress) the vegetation ranges from stunted upper montane forest (9–10 m) to tufts of dwarf-scrub barely 0.3 m tall. Although in the cloud-zone, high wind velocity coupled with high altitude renders this a habitat with great temperature and moisture regime extremes. Similar soils occur in the summit zone of Mount Tambuyukon (2300–2570 m), and here a unique (species-rich) graminoid scrub with many endemics has developed despite the soils having such high Mg:Ca quotients and phytoavailable Ni and Mn. Therefore, altitude plays a significant role in the ultramafic stress that soils exert on the vegetation.

The most common soils in Kinabalu Park are montane Cambisols (Dystric Cambisols) that occur on moderate to steep slopes at altitudes of 900–2500 m. Particularly in the cloud forest zone, there is a thick build-up of mor humus at the surface and in some flatter and wetter areas, *sphagnum* peat. The typical vegetation is either open lower montane forest (>1800 m) or dense upper montane forest ('cloud forest') at altitudes 1800–2500 m. These soils are acidic (pH 4.5–5.8) with low CEC and intermediate Mg:Ca quotients. These soils are very widespread in Kinabalu Park and cover most (steep slopes) of ultramafic bedrock outcrops. The formation of peat on shoulders has been attributed to the frequency of cloud-cover and hence the continuous saturation of the soil (Proctor et al., 1988). These ultramafic soils are fairly similar to the non-ultramafic soils at the same altitude and, as a consequence, few plant species are unique to the ultramafic equivalents, although stunting is more pronounced, probably due to the still unusual geochemistry: high Mg:Ca, low K and P contents, high Ni availability (Borhidi 1988; Proctor et al. 1999) because these environments are humid and the vegetation unlikely suffers from water stress. The ultramafic soils at Marai Parai (1550–1700 m) on Mount Kinabalu's west face are constantly waterlogged from water percolating from the granite summit plateau that towers above. As a result, there is peat formation and acidification of these soils and the vegetation is a graminoid scrub resembling that of the summit region of Mount Tambuyukon at much higher altitude, despite entirely different soil chemistries. They probably resemble the "sols à accumulation humifères" described in New Caledonia above 900 m in many ways, including the low pH (Latham 1975a). The lack of trees might be explained by the combination of waterlogging and extremely high concentrations of exchangeable Al that are likely to be phytotoxic at pH below 5.2, although waterlogging is probably the most predominant factor.

504 Finally, deep laterite soils (Geric Ferralsols) occur in low-lying areas in valleys and on plateaus
505 where flat surfaces occur which allow for these old and intensively weathered soils to occur
506 (Echevarria, 2017). Although not widespread in the mountainous terrain of Kinabalu Park, these
507 types of ultramafic soils are common elsewhere in Sabah and also in many tropical settings
508 including (Latham 1975b; Becquer et al. 2001; Proctor 2003; Garnier et al. 2009), and are
509 particularly well developed on the Mount Tawai Plateau near Telupid. These are ‘lateritic’ red deep
510 soils (up to 36 m has been observed at a road excavation), well-drained and frequently have marked
511 iron concretions (ferricrete: plinthic or petroplinthic surface horizons) on the surface. Pseudo-total
512 concentrations of Fe and Cr are extremely high, CEC is very low, 2:1 clay minerals are absent from
513 the soil profiles, and concentrations of extractable (*i.e.* plant-available) trace elements (Ni, Co, Cr)
514 are all low. The Mg:Ca quotient is generally low due to long and intense weathering which
515 completely washes Mg out, but not Ca. These soils are not likely to have major effects on the
516 vegetation and do not show additional geochemical stress than in other laterites formed on non-
517 ultramafic materials. Only the presence of available Cr-VI amounts in ultramafic laterites can have
518 some toxic effect on the biota, but it is absolutely not documented (Garnier et al., 2009). The
519 vegetation on these soils (particularly on undulating terrain and plateaux) is very tall dipterocarp-
520 forest with a sparse understorey of tree saplings but virtually no herbs. Despite very low
521 concentrations of (plant-available) nutrients, including P, Ca and K, these soils support very high
522 biomass ecosystems. Most nutrients are contained in the living biomass, and recycling from leaf
523 litter mass is fast (as evidenced by the distinct absence of any significant leaf litter accumulation)
524 and efficient (as indicated by the high densities of surface roots). Geric Ferralsols are the most
525 benign in terms of their chemical properties, notwithstanding they are (very) nutrient-poor although
526 that in itself is not unique, as (lowland) rainforests (on non-ultramafic Ferralsols) soils are generally
527 nutrient-poor (Whitmore 1975; Vitousek and Sanford 1986), Experimental work on these ultramafic
528 rainforest soils has shown that nutrient-limitation rather than toxicity is likely important here
529 (Proctor et al. 1999; Brearley, 2005).

530 The three major serpentinite occurrences in Kinabalu Park are located in the Wuluh Valley, the
531 Bambang Valley and the Panataran Valley. At these locations, rivers cut through the formations,
532 which originally formed along major fault lines (and such topographic weaknesses are exploited by
533 the rivers in the present day). These fault lines were fissures during emplacement through which
534 water could circulate and interact with peridotite rock resulting in serpentinisation. Serpentinic
535 soils occur mainly on (extremely) steep slopes facing the respective rivers. At these localities,
536 massive serpentinite bedrock crops out and is undercut by a river, causing cascades of landslides of
537 fresh rock debris. The unweathered debris is rich in fine particles including mostly clay minerals
538 (talc, smectite) but these soils have very shallow development and little weathering features, which

classifies them as Hypereutric Leptosols (Hypermagnesian), the least developed ultramafic soils of all. They usually develop on less than 20 cm and lack a Bw horizon. The older soils on ridges and old landslides have a thicker layer of organic matter (O-horizon) mainly made up of ‘needles’ of *Ceuthostoma* sp. (Casuarinaceae) trees which decompose slowly, with a developed A₁-horizon (<20 cm) and unaltered serpentinite debris underneath (C horizon). The soil pH ranges from 6.5 in the soils rich in organic matter to pH 9.8 in the unweathered soil (C horizon and further down the profile (>50 cm), which are extreme values for soils, comparable to those of saline soils. Some of these serpentinitic Hypereutric Leptosols have extremely high carboxylic acid extractable Cr concentrations. The high phytoavailable Cr concentrations in these soils is mostly due to Cr-VI that is formed during Mn oxide reduction in the clay-dominated horizons of tropical ultramafic soils (Garnier et al. 2009; Raous et al. 2013). Such available Cr-VI concentrations could produce toxic effects on the vegetation that could be even more adverse than available Ni pools (Reference???). Some mixed soil types also exist, in particular Bambang and Mesilau (moderately deep montane soils with mor humus buildup overlying on serpentinite bedrock), and Bukit Hampuan (also serpentinite bedrock, but drier eroded soils). The intermediate properties of these soils are reflected in their soil chemistry (relatively high pH, high Mg:Ca) as well as in the vegetation these soils support (frequent occurrence of *Ceuthostoma* sp. – Casuarinaceae – indicative of serpentinite and high pH).

All four types are clearly distinguished by statistical analyses, which underlines their significance in terms of soil classification and later on for the interpretation of soil-vegetation relationships. In comparison with other tropical ultramafic soils from around the world (Table 9), the ultramafic soils from Kinabalu Park are very diverse in their chemical properties, and some of the extractable concentrations of Ni, Co and Cr were recorded as exceptionally high. They usually show broader ranges of all parameters than any of the reported sites, except for total Ni (see data for Brazil). In particular, the existence of soils with strongly alkaline pH (*i.e.* Hypereutric Leptosols) is not reported elsewhere in tropical ultramafic regions. Although extractable Cr was highest in Hypereutric Leptosols, pseudo-total Cr was highest in Geric Ferralsols (at the Serinsim site) and comparable to the very high values found in New Caledonian or Brazilian soils.

4.2. Effects of bedrock serpentinisation and weathering on soil types

In the literature, soils derived from either peridotite or serpentinite bedrock are often called ‘serpentine soils’ and botanists and ecologists commonly do not distinguish between these two types (as emphasised by Alexander 2004; 2009). Although arguments have been made to term

574 'serpentine soils' more generally 'ultramafic soils', which is geologically correct and avoids
575 confusion with 'serpentinite', the term is cemented in the field and in literature (Brooks 1987). The
576 differences between soils derived from 'peridotite' and 'serpentinite' are ecologically important, but
577 they form a complex matrix of soil pedological and chemical properties that depend on weathering,
578 altitude and topography (Jaffré 1980; Proctor et al. 1999; Kierczak et al. 2016; Echevarria 2017). It
579 was hypothesized that soils derived from bedrock with a higher degree of serpentinisation result in
580 soil chemistries with more adverse properties to plant life (Kierczak et al. 2016; Echevarria 2017).
581 Two types of soils turned out to have extreme chemical properties however: (i) soils derived from
582 peridotite at high altitude – (Hyper)Eutric Cambisols (Hypermagnesian) – where rejuvenation
583 through erosion maintains soils at an early weathering stage (Echevarria, 2017), and (ii) soils
584 derived from strongly serpentinised bedrock – serpentinitic Hypereutric Leptosols (Hypermagnesian)
585 – whose evolution is slow because of their unusual mineralogical composition (*i.e.* dominated by
586 slowly-weathered serpentine and talc minerals).

587
588 Fully developed laterites (Geric Ferralsols) show much lesser influence of the original ultramafic
589 material. For instance, pH values, exchangeable Ca over exchangeable Mg, exchangeable Ni are
590 more similar to other Ferralsols developed on non-ultramafic materials. In Ferralsols, Ni is borne
591 mainly by crystallised Fe-oxides and the resulting availability is extremely low (Becquer et al.
592 2006; Massoura et al. 2006; Raous et al. 2013). In contrast, Cr-VI available pool can be
593 significantly elevated ($>1000 \mu\text{g g}^{-1}$) also in these soils (Garnier et al. 2009; Raous et al. 2013) and
594 thus represent a significant constraint for the vegetation, especially with the lack of phosphorus due
595 to ultramafic conditions. The chromate ions in excess interfere with the uptake of phosphate ions by
596 plants. This geochemical stress for plants that is only found in ultramafic laterites has not been
597 investigated thoroughly, although could be a major pressure for plant adaptation.

598 599 **4.3 How ultramafic soil diversity does influence floristic patterns?**

600 Deep laterite soils (Geric Ferralsols) developed on undulating terrain, either over peridotite or
601 strongly serpentinised peridotite, were characterised by extremely high pseudo-total Fe and Cr, low
602 CEC (0.1–2 cmol/kg), acidic (pH 4.5–5.5) and low exchangeable Mg (but also low exchangeable
603 Ca and K). Distribution: Serinsim, Nalumad. These deep ultramafic Geric Ferralsols support tall
604 species-rich rainforest, not dissimilar to podzolised sandstone nutrient-poor forests elsewhere in
605 Sabah, with the dipterocarps *Shorea laxa* and *Shorea venulosa* and the gymnosperm *Agathis*
606 *borneensis* (Araucariaceae) dominating. Other characteristic dipterocarps include *Dipterocarpus*
607 *lowii*, *D. ochraceus*, *Shorea kunstleri*, *S. laxa*, *S. lowii*, *S. tenuiramulosa*, *S. venulosa* and
608 *Dryobalanops beccarii* (Acres et al. 1975; Ashton 1982). Comparable rainforests growing on Geric

609 Ferralsols at low altitude (because of the lack of water limitation) are found in the area of Moa in
610 Cuba (Borhidi 1988), in alluvial soils of Rivière Bleue in New Caledonia (Jaffré 1980, 1992; Isnard
611 et al. 2016) and in the Philippines, despite a high rainfall, there is no such forest development as in
612 this region of Sabah. Some authors suspect that fire is involved in the lack of forest development on
613 Ferralsols that can be observed in many places with no apparent effect of edaphic conditions
614 (Proctor 2003). It is clearly the fact in New Caledonia, where the rainforest is now limited to
615 alluvial plains in low altitudes (Isnard et al. 2016).

616

617 Moderately deep montane soils (Dystric Cambisols) frequently with high build-up of organic matter
618 (mor humus) are acidic (pH 5–6), have with high exchangeable Al, but low CEC (1–3 cmol kg⁻¹)
619 and high pseudo-total Fe, Cr and Ni. Distribution: Mesilau, Bukit Babi, Bambang, Marai Parai,
620 Bukit Hampuan, Mount Tambuyukon (slopes), Mount Nambuyukon. The Dystric Cambisols are the
621 most widespread soils in the ‘cloud-forest’ zone of Kinabalu Park. The tree density is generally
622 high and these ecosystems have high species diversity, particularly in epiphytes such as orchids.
623 The vegetation is typical for this altitudinal zone, and dominated by trees in the families Myrtaceae,
624 Fagaceae, Podocarpaceae and Rubiaceae. The vegetation, however, differs little from soils derived
625 from non-ultramafic bedrock in the same area, although physiognomy is often more stunted on the
626 ultramafic soils for reasons not fully understood. Strongly serpentinized soils on high altitude
627 (Bukit Hampuan, Bambang, Mesilau) have Dystric Cambisols, but these are much more base-rich
628 (CEC, pH) and have higher Mg:Ca quotients compared to peridotite-derived ultramafic soils or
629 non-ultramafic soils, which is reflected in extremely species-rich vegetation.

630

631 Very shallow skeletal soils on high-altitude (2400–2950 m) weathered peridotite with very little
632 organic matter (Eutric/Hypereutric Cambisols Hypermagnesian). These soils are very young and
633 rejuvenated by erosion and are characterised by extremely high pseudo-total and exchangeable Mg,
634 low CEC (3–5 cmol kg⁻¹), very high extractable Ni (50–180 µg g⁻¹ DTPA-Ni) and Mn (250–500
635 µg g⁻¹ DTPA-Mn), and are moderately acidic (pH 5–5.8). Distribution: Mount Tambuyukon
636 (summit), Layang-Layang. The skeletal Eutric Cambisols are extreme in their chemical properties
637 (high Mg:Ca, high extractable Ni and Mn), and coupled with high altitude (2400–2950 m) have
638 given rise to very stunted vegetation dominated by species in the Myrtaceae and Podocarpaceae at
639 Layang-Layang on Mount Kinabalu’s south slope. On the more exposed slopes, the vegetation is
640 co-dominated by just two plant species, *Leptospermum recurvum* (Myrtaceae) and *Dacrydium*
641 *gibbsiae* (Podocarpaceae), both endemic. Locally, the carnivorous pitcher plant *Nepenthes villosa*
642 (Nepenthaceae), also endemic, is common. The ultramafic graminoid vegetation (<1 m high) on the
643 exposed summit ridges of Mount Tambuyukon is unique and not found anywhere else in Sabah or

644 Borneo. This vegetation type is characterized by a range of shrubs such as *Tristaniaopsis elliptica*
 645 (Myrtaceae), *Lithocarpus rigidus* (Fagaceae), *Ternstroemia lowii* (Pentaphylacaceae), *Scaveola*
 646 *verticillata* (Goodeniaceae), *Wikstroemia indica* (Thymelaeaceae), *Leptospermum recurvum*
 647 (Myrtaceae), *Podocarpus brevifolius* and *Dacrydium gibbsiae* (Podocarpaceae), the sedges, *Gahnia*
 648 *javanica* and *Schoenus melanostachys*.
 649
 650 Soils developed on bare serpentinite (serpentinitic hypermagnesian Leptosols) at low altitude (400–
 651 700 m) have high total and exchangeable Mg (Mg:Ca 5–25), very high CEC (15–25 cmol kg⁻¹),
 652 high extractable Ni (20–50 µg g⁻¹ DTPA Ni) and circum-neutral pH (6.5–7.5) near the surface and
 653 highly alkaline at depth (pH 8–9.5). Distribution: Panataran Valley, Wuluh River. The serpentinitic
 654 Leptosols give rise to a mosaic of landslides, with the older landslides and the ridges having open
 655 medium-tall forest dominated by Casuarinaceae (*Gymnostoma sumatranum*, *G. nobile* and
 656 *Ceuthostoma terminale*) whereas the younger landslides have pioneer communities often with
 657 shrubs of *Scaevola micrantha* (Goodeniaceae), *Decaspermum vitis-idaea* (Myrtaceae) and
 658 *Macaranga kinabaluensis* (Euphorbiaceae). Two terrestrial hyper-endemic orchids, *Paphiopedilum*
 659 *rothschildianum* and *P. dayanum*, are restricted to this pioneer vegetation. Another hyper-endemic,
 660 the tree *Borneodendron aenigmaticum* (Euphorbiaceae), co-occurs with Casuarinaceae in more
 661 developed forest. It is difficult to compare these soils with other regions in the world. In the region
 662 of Moa of Cuba, these soil types (Cambic Leptosols or Hypereutric Leptic Cambisols) are those
 663 which display the highest rate of endemism (Borhidi 1988).
 664
 665 Numerous experimental studies have demonstrated Ni-toxicity in plants in ultramafic soils (for
 666 example L'Huillier et Edighoffer. 1996; Kukier and Chaney 2001), but some rare plant species
 667 actually thrive in Ni-rich soils. These plants, nickel hyperaccumulator species, plants that sequester
 668 in excess of 1000 µg g⁻¹ Ni in their shoots (Van der Ent et al. 2013) are also known from Sabah
 669 (Proctor et al., 1988; Van der Ent et al., 2016b). Their occurrence in Sabah (van der Ent et al.,
 670 2016a) is restricted to soils with exceptionally high available Ni, mainly strongly serpentinised soils
 671 in the lowlands (<1200 m asl). These occurrences are localized on very shallow soils with active
 672 mineral weathering. In such soils, the dissolution of primary minerals releases Ni, which is then
 673 made available by adsorption onto high CEC clays and non-crystallised Fe-oxides. This allow Ni
 674 exchangeable pools to be high enough to favour Ni hyperaccumulation by specialised species, for
 675 example in Nalumad where the strongly serpentinised soils also have very high pseudo-total Mn
 676 (8698–16 120 µg g⁻¹) and up to 300 µg g⁻¹ DTPA-Mn and 276–654 µg g⁻¹ DTPA-Cr. The
 677 occurrence of Ni-hyperaccumulators in ultramafic areas of Sabah has been shown to be strictly
 678 correlated with high-Mg soils and it was never reported on laterites (van der Ent et al., 2016a).

679

680 Finally, as reported in other studies from other tropical ultramafic regions of the world, the floristic
681 zonation with altitude is more pronounced on ultramafic substrates than on non-ultramafic
682 substrates. It is the case for example in the region of Moa (Borhidi 1988) and also in Mount Silam
683 in Sabah (Proctor 2003). The reasons why it is the case are probably due to the geochemistry of the
684 soils (altitude soils are mostly Dystric or Hypereutric Cambisols because of the slope that
685 rejuvenerates the profiles).

686

687 **5. CONCLUSIONS**

688 The occurrence and chemical characteristics of these soils are a function of bedrock mineralogy
689 (serpentinisation), weathering and landscapes attributes (altitude, slope). Overall, ultramafic soils
690 are less acidic, have higher EC, higher pseudo-total Ca, Co, Cr, Fe, Mg, Mn and Ni, higher
691 exchangeable Ca and Mg, higher Mg:Ca quotients, similar exchangeable K, higher DTPA-
692 extractable Co, Cr, Cu and Ni, and lower chemically-extractable P than adjacent non-ultramafic
693 soils. Well-developed Geric Ferralsols probably show less differences from non-ultramafic soils
694 under similar conditions than high altitude soils or shallow erosion-rejuvenated Cambisols.
695 Therefore they host ecosystems that show little difference with those present in soils developed on
696 other types of bedrocks. On the contrary, ultramafic Leptosols or shallow hypermagnesian Cambisols
697 that form on serpentinite substrates host specific and adapted vegetation (high level of endemism)
698 that tolerates geochemical peculiarities, including Ni hyperaccumulators. Whether soils are
699 moderately or weakly weathered due to the original mineralogy (i.e. strongly serpentinised bedrock)
700 or due to lack of evolution (high-slope erosion/rejuvenation), the so-called 'serpentine syndrome'
701 only seems to be restricted to these two types of soils. However, the geochemical Cr anomaly (i.e. high
702 levels of exchangeable Cr-VI) of ultramafic laterites probably exerts strong effects on the
703 vegetation but this has never been studied. The lack of strong differences with lowland forests on
704 other geological substrates tends to hide this phenomenon.

705

706 The highest level of edaphic stress is therefore concentrated on fully serpentinised ultramafic
707 outcrops, which should be prioritised areas for the search for endemic plants on ultramafic
708 substrates in Sabah and other tropical regions.

709

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999

1000

1001 **FIGURES**

1002

1003 **Figure 1.** Geological map of the study area with sampling sites marked (coloured circles)

1004

1005 **Figure 2.** Stacked XRD profiles for rock specimens, with diagnostic peaks and Miller indices
1006 provided for constituent minerals. ACT = actinolite (here tremolite – an amphibole), ENST =
1007 enstatite (a pyroxene), DIOP = diopside (a pyroxene), FOR = forsterite (Mg-rich olivine), MAG =
1008 magnetite, SERP = serpentine, SPIN = spinel, TALC as written.

1009

1010 **Figure 3.** Stacked XRD profiles for soil samples with diagnostic peaks and Miller indices provided
1011 for constituent minerals. ACT = actinolite (here tremolite – an amphibole), ENST = enstatite (a
1012 pyroxene), DIOP = diopside (a pyroxene), FOR = forsterite (Mg-rich olivine), MAG = magnetite,
1013 SERP = serpentine, SPIN = spinel, TALC, GOE = goethite, CHL = chlorite, and QTZ = quartz as
1014 written.

1015

1016 **Figure 4.** Partitioning of Ni, Cr, Co over soil fractions (as percentage of total) of the four main soil
1017 types (EX = water soluble and exchangeable, Mn-OX = bound to Mn oxides, AM-Fe = bound to
1018 amorphous Fe oxides, CR-Fe, bound to crystalline Fe oxides, Res = residual.

1019

1020 **Figure 5.** NMDS of pseudo-total soil elements (A) and exchangeable and extractable elements (B)
1021 from all collection sites, contrasted with non-ultramafic comparison soils. The 4 main soil types are
1022 nominally outlined in the NMDS-plots (based on site typology).

1023

1024

1025

1026 **TABLES**

1027

1028 **Table 1.** Collection localities with environmental and pedological attributes (bedrock types, soil
1029 classes, soil depth).

1030

1031 **Table 2.** Bedrock chemistry (ranges and means) of ultramafic and non-ultramafic bedrock total
1032 values (pressurised HF/HCl/HNO₃ microwave digest).

1033

1034 **Table 3.** Chemistry of ultramafic and non-ultramafic soils. Abbreviations: 'pseudo-total'
1035 microwave-assisted digestion with HNO₃ and HCl, 'DTPA' is DTPA-extractable metals, 'ML-3' is
1036 Mehlich-3 extractable P, and 'exch.' is exchangeable with silver-thiourea.

1037

1038 **Table 4.** Soil pseudo-total elements of the main 'ultramafic edaphic islands' in $\mu\text{g g}^{-1}$ or mg g^{-1} if
1039 marked with asterisk (as means from unpressurised HNO₃/HCl microwave digests).

1040

1041 **Table 5.** Soil extractable (carboxylic acid) elements (Co, Fe, Mn, Ni) in $\mu\text{g g}^{-1}$, exchangeable
1042 elements (Al, Ca, K, Mg, Na) in $\text{cmol}^{(+)} \text{kg}^{-1}$ and Mehlich-3 extractable P ($\mu\text{g g}^{-1}$), all as means.

1043

1044 **Table 6.** XRD modelled mineral relative abundances for selected rocks, assuming the sample is a
1045 mixture of crystalline diopside, tremolite (actinolite), antigorite, lizardite, spinel, talc, fosteritic
1046 olivine, and smectite group clay minerals. Total elemental concentrations in selected rock samples
1047 ($\mu\text{g g}^{-1}$ or % if indicated).

1048

1049 **Table 7.** XRD modelled mineral relative abundances for selected soils, assuming the sample is a
1050 mixture of crystalline diopside, tremolite (actinolite), antigorite, lizardite, spinel, talc, fosteritic
1051 olivine, and smectite group clay minerals. Pseudo-total elemental concentrations in selected soil
1052 samples ($\mu\text{g g}^{-1}$).

1053

1054 **Table 8.** Soil profiles: pseudo-total values for soil in $\mu\text{g g}^{-1}$ or mg g^{-1} (elements marked with
1055 asterisk) total values for bedrock in % (Ca, K, Mg, Al, Fe, Si) and $\mu\text{g g}^{-1}$ (Co, Cr, Mn, Ni, P).

1056

1057 **Table 9.** Chemistry of tropical ultramafic soils from around the world. CEC and exchangeable
1058 cations with silver-thioreia, 2 CEC and exchangeable cations with ammonium acetate, 3 Olsen-P
1059 extract (NaHCO₃), 4 Soil digestion with HNO₃/HCl, 5 Ammonium acetate extract, 6 Acetic acid
1060 extract/digestion, 7 Bray's extract, 8 DTPA-extract, 9 Mehlich-3 extract.

TABLE 1

Site number	Locality	n (soils)	Altitude range (m asl)	Slope (%)	Bedrock type	Soil class	Soil depth (m)	O–A–horizon
1	Mt Tambuyukon (summit)	53	2318–2534	20–50	Peridotite (Dunite)	Eutric Leptic Cambisol (hypermagnesian)	<0.3	Absent
2	Mt Tambuyukon (slopes)	12	1466–1906	<20	Peridotite	Dystric Follic Cambisol (magnesian)	<0.5	Mor accumulation
3	Wuluh River	35	750–820	50–75	Serpentinite	Mollic Leptosol (colluvic, hypermagnesian)	>1	Thin A–horizon
4	Serinsim	15	612–671	<20	Peridotite	Plinthic Geric Rhodic Ferralsol	>5	Only leaf litter, iron concretions
5	Mt Nambuyukon	9	1584–1590	<20	Serpentinite	Dystric Ferralic Cambisol	<1	Thin A - horizon
6	Panataran Valley	26	588–781	20–50	Serpentinite	Mollic Leptosol (hypermagnesian)	> 1	Thin A - horizon
7	Marai Parai	34	2633–1753	<20	Peridotite	Dystric Leptic Cambisol	<0.3	Thin A - horizon
8	Layang–Layang	31	2305–2950	20–50	Non-serpentinised Peridotite	Eutric Leptic Cambisol (hypermagnesian)	<0.3	Absent
9	Mesilau	25	1909–2067	<20	Partially serpentinised Peridotite with Tremolite	Follic Hypereutric Cambisol (hypermagnesian)	<1	Mor accumulation
10	Bukit Babi	18	1877–2286	20–50	Peridotite	Dystric Follic Cambisol (hypermagnesian)	<1	Mor accumulation
11	Bambangan	27	1683–2077	50–75	Serpentinite	Mollic Leptosol (hypermagnesian)	<1	Thin A–horizon
12	Bukit Hampuan	28	963–1336	50–75	Mixed	Mollic Leptosol (hypermagnesian)	0.5–1	Thin A–horizon
13	Nalumad	12	754–836	<20	Peridotite	Plinthic Rhodic Ferralsol (magnesian)	>5	Only leaf litter, iron concretions

TABLE 2

Ultramafic	Unit	Ultramafic bedrock (n = 76)		Non-ultramafic bedrock (n = 13)	
Al	%	0.02–19	3	0.1–10	5
Ca	%	0.01–12	2	0.002–10	1
Co	µg g ⁻¹	3–27	8	3–11	5
Cr	µg g ⁻¹	8–8604	1441	11– 906	188
Cu	µg g ⁻¹	0.1–620	46	0.1–170	25
Fe	%	0.06–43	5	0.1–5	2
K	%	0.01–3	0.3	0.01–2	1
Mg	%	0.05–53	19	0.1–28	5
Mn	µg g ⁻¹	31–3264	1237	31–2869	560
Na	%	0.01–3	0	0.02–2	1
Ni	µg g ⁻¹	16–4775	939	15–1315	225
P	µg g ⁻¹	2.3–804	72	40–571	142
S	%	0.01–0.11	0.05	0.01–0.1	0.1
Si	%	0.4–36	15	2–36	21
Zn	µg g ⁻¹	3.5–208	59	4–148	43

TABLE 3

Ultramafic	Extract	Unit	Ultramafic soils (n = 423)		Non-ultramafic soils (n = 67)	
Al	Total	mg g ⁻¹	1.2–118	19	0.3–92	19
Ca	Total	µg g ⁻¹	7.7–39300	2433	2.2–12380	541
Co	Total	µg g ⁻¹	0.5–1524	253	0.5–26	7.7
Cr	Total	µg g ⁻¹	121–21710	3873	2.4–170	36
Cu	Total	µg g ⁻¹	2.4–453	47	0.04–83	16
Fe	Total	mg g ⁻¹	21–535	144	0.1–121	16
K	Total	µg g ⁻¹	< 0.1–1056	93	38–7297	1065
Mg	Total	mg g ⁻¹	0.3–235	32	0.03–18	1.9
Mn	Total	mg g ⁻¹	0.04–34	3	< 0.01–1.5	0.1
Na	Total	µg g ⁻¹	< 0.1–361	146	2.4–132	55
Ni	Total	µg g ⁻¹	17–9308	1623	0.5–338	28
P	Total	µg g ⁻¹	4.4–585	127	20–532	121
S	Total	µg g ⁻¹	33–6172	371	64–641	212
Zn	Total	µg g ⁻¹	13–373	107	1.2–111	19
pH	1:2.5 H ₂ O	–	3.8–9.7	6.0	3.5–7.2	4.6
EC	1:2.5 H ₂ O	µS	9.0–939	165	18–291	74
Al	DTPA	µg g ⁻¹	0.03–522	14	2.5–850	337
Ca	Exch.	µg g ⁻¹	0.6–6946	402	17–3394	125
Co	DTPA	µg g ⁻¹	0.04–96	17	< 0.1–0.9	0.2
Cr	DTPA	µg g ⁻¹	< 0.1–13	0.4	< 0.1–0.7	0.1
Cu	DTPA	µg g ⁻¹	< 0.1–26	1.7	< 0.1–7.4	0.7
Fe	DTPA	µg g ⁻¹	0.5–873	96	2.9–737	159
K	Exch.	µg g ⁻¹	0.7–307	36	2.5–191	38
Mg	Exch.	µg g ⁻¹	1.8–9155	942	0.2–57	12
Mn	DTPA	µg g ⁻¹	0.4–822	215	0.1–40	3.6
Na	Exch.	µg g ⁻¹	1.5–1652	103	0.2–89	11
Ni	DTPA	µg g ⁻¹	0.2–442	62	0.03–3.3	0.3
P	ML-3	µg g ⁻¹	< 0.1–32	2.7	1.7–80	12
S	DTPA	µg g ⁻¹	0.9–683	24	1.0–33	6.5
Zn	DTPA	µg g ⁻¹	0.02–161	1.2	0.05–16	0.9
Mg:Ca	Exch.	–	< 0.1–82	5.3	< 0.1–1.0	0.2

TABLE 4

Site	n	pH	Al*	Ca	Co	Cr*	Fe*	K	Mg*	Mn*	Ni
Bambangan	27	6.2	22.5	5990	214	3.7	95.8	75	40	2.8	1090
Bukit Babi	18	5.5	11.8	654	162	3.1	70.9	29	13	2.2	346
Bukit Hampuan	28	6.2	26.6	4028	318	4.7	137.8	90	28	3.9	1798
Layang-Layang	31	5.1	11.6	867	120	0.6	86.9	148	12	1.5	956
Marai Parai	34	5.3	21.3	698	69	3.4	75.8	44	24	0.7	442
Mesilau	25	6.2	12.4	909	156	0.7	78.6	136	57	2.0	1409
Serinsim	15	4.7	30.8	561	50	16.3	385.7	83	0.5	2.3	2452
Mt Tambuyukon summit	53	6.0	6.3	882	464	3.2	216.8	96	12.0	6.4	2137
Mt Tambuyukon slopes	12	5.5	17.9	651	737	8.8	312.0	83	4.9	7.7	2476
Wuluh River	35	7.3	5.5	1761	177	2.5	72.7	65	120	2.3	2268
Mt Nambuyukon	9	5.2	60.7	1186	165	3.8	188.2	87	6.2	2.1	779
Nalumad	12	4.6	31.4	578	124	6.1	233.2	160	0.6	3.1	902
Panataran Valley	26	6.5	26.5	9324	242	2.5	122.3	102	56	3.3	1496

TABLE 5

Site	n	Co	Fe	Mn	Ni	Al	Ca	K	Mg	Na	Mg:Ca	CEC	P
Bambangan	27	15	443	236	34	0.02	1.7	0.09	9.9	0.3	8.1	12.0	2.7
Bukit Babi	18	32	388	583	20	0.02	0.7	0.10	1.3	1.0	2.4	3.2	2.0
Bukit Hampuan	28	36	633	435	68	0.03	5.1	0.13	13.8	0.7	11.7	19.8	4.0
Layang-Layang	31	11	388	226	21	0.20	0.8	0.10	1.7	0.5	6.0	3.4	4.0
Marai Parai	34	4	98	73	13	0.12	0.3	0.05	1.0	0.1	3.8	1.6	1.8
Mesilau	25	9	616	157	31	0.02	1.3	0.08	10.1	0.2	12.8	11.8	3.5
Serinsim	15	2	73	30	3	0.04	0.3	0.08	0.2	0.1	0.8	0.6	1.3
Mt Tambuyukon summit	53	106	560	1512	139	0.01	1.1	0.09	3.5	1.1	5.7	5.8	1.1
Mt Tambuyukon slopes	12	156	528	1542	38	0.01	0.4	0.07	1.1	1.3	10.4	2.8	1.4
Wuluh River	35	20	553	259	152	0.09	1.2	0.06	14.6	0.1	21.4	16.0	2.3
Mt Nambuyukon	9	15	104	166	3	1.17	0.7	0.05	0.4	0.3	0.8	2.6	1.7
Nalumad	12	29	121	311	7	1.32	0.3	0.11	0.2	0.4	1.2	2.3	2.5
Panataran Valley	26	25	671	370	66	0.01	4.8	0.11	16.3	0.6	5.3	21.9	2.9

TABLE 6

Locality	Layang-Layang	Bambangan	Mt. Tambuyukon (summit)	Mt. Tambuyukon (summit)	Mesilau
Site number	8	11	1	1	9
diopside	21.8	4.5	0.4	3.1	4.9
tremolite	5	2.6	0.3	2.4	10.7
antigorite	28.6	29.1	32.1	24.3	23.8
lizardite	7.5	17.8	26.8	27.2	12.9
spinel	2.9	8.1	5.7	7.3	9.2
talc	4.2	4.9	1.5	2.7	5.5
forsterite	29.7	32.6	33	32.6	32.6
smectite group clays	0.3	0.4	0.3	0.3	0.4
Al %	1.7	1.1	0.03	0.02	0.4
Ca %	4.4	0.2	0.02	0.2	0.7
Co	6	8	9	8	10
Cr	1287	2735	239	212	1571
Cu	19	36	13	33	5
Fe %	6.1	5.6	2.5	4.5	5
K %	0.02	0.007	0.009	0.003	0.005
Mg %	20.4	29.4	16.5	24.7	22.2
Mn	1394	1287	867	1089	1486
Na %	0.08	0.01	0.03	0.01	0.01
Ni	775	1205	1265	1266	1078
P	52	25	13	23	27
S %	0.04	0.09	0.06	0.02	0.04
Si %	14.5	16.1	13.4	12.5	9.3
Ti	963	124	31	22	85
Zn	45	75	44	59	69

TABLE 7

Locality	Bambangan	Bukit Babi	Layang– Layang	Marai Parai	Mesilau	Mt Tambuyukon	Mt Tambuyukon	Wuluh River	Serinsim
Site number	11	10	8	7	9	1	1	3	4
diopside	0.5	1.4	3.5	1.1	2.8	1.3	2.4	0	1.5
tremolite	12.7	22.4	22.8	17.2	25.9	13.7	16.5	0	17.3
antigorite	21	28.1	24.5	25.9	23.1	22.4	19.2	23.1	18
lizardite	9	9.7	8.7	8.4	7.5	11	7.6	35.1	6.7
spinel	8	5.8	10.4	6	7.4	14.1	13.6	10.9	28.9
talc	27.2	11.5	1.9	15.3	11.1	7.5	17.1	1.8	5
forsterite	20.6	19.7	17.8	24.9	20	28.6	22.5	28.7	21.4
smectite group clays	1	1.5	1.4	1.2	2.2	1.3	1.1	0.4	1.1
Al*	28.7	26.8	39.7	18.9	29.5	5.4	6.5	2.1	33.5
Ca	3990	670	2524	446	2788	510	325	75	28
Co	236	102	63	72	176	417	185	103	4
Cr	4071	2800	474	4934	1176	1742	1494	899	10530
Cu	21	13	56	21	28	15	7	3	50
Fe*	101.6	88.4	73	216.1	155.4	238.2	164.5	43	349
K	19	56	1904	23	68	32	39	< 0.01	< 0.01
Mg*	30.2	42.1	11.8	15	35.3	13.4	6.4	198.7	1.5
Mn	4115	1441	748	1193	2534	7582	3120	922	2508
Na	61	16	113	< 0.01	115	53	37	< 0.01	< 0.01
Ni	641	487	236	773	1368	2031	1109	1131	2609
P	77	62	167	81	130	116	42	11	205
S	318	343	531	395	296	415	367	89	1881

TABLE 8

Depth (m)	pH	EC	Ca	K	Mg	Mg:Ca	Al*	Co	Cr*	Fe*	Mn	Ni	Ni ML-3	P	Si
Sunsui															
0–5	4.4	55	224	13	17	0.1	16	5	0.9	76	96	55	1.1	43	–
5–9	5.7	12	226	13	237	1.1	19	18	1.0	98	408	144	3.5	35	–
5–9	5.8	169	611	51	2142	3.5	27	150	1.1	109	3157	1478	92	142	–
9–10	6.1	891	667	34	3996	6.0	17	66	0.8	51	467	1960	318	51	–
10–14	6.3	196	744	129	4852	6.5	17	114	0.9	102	2014	1810	52	100	–
14–18	6.7	100	905	57	6179	6.8	18	180	0.8	91	2043	2083	43	104	–
18–22	6.9	195	1043	90	3423	3.3	6	157	0.8	86	1648	3072	111	32	–
Bedrock	–	–	6	1	420	–	9	70	694	68	1210	953	–	49	226
Hampuan															
0–4	6.0	18	231	13	18	0.1	100	878	14.6	395	6931	2509	0.4	106	–
4–7	6.2	10	230	13	137	0.6	92	671	15.8	383	7033	3583	2.1	92	–
7–16	5.6	13	220	16	31	0.1	89	1055	15.8	372	8106	3101	0.7	74	–
16–26	6.5	55	465	9.2	3389	7.3	37	1040	14.0	352	8728	6985	44	47	–
26–30	7.6	85	686	11	6312	9.2	13	694	5.1	254	7540	9308	102	41	–
30–36	7.2	132	950	5.2	9155	9.6	34	597	9.0	176	7512	7164	129	20	–
Bedrock	–	–	12	0.2	126	–	7	8	1244	23	1032	963	–	67	3.9
Serinsim															
0–0.1	5.1	74	207	29	28	0.1	33	151	17.6	426	4754	2532	19	443	–
0.3–0.4	5.3	55	208	14	12	0.1	31	19	16.9	407	3243	2622	1.9	149	–
0.8–0.9	5.3	29	212	6.6	10	0.0	36	181	19.9	453	3493	3205	0.7	186	–
Bedrock	–	–	0.4	0.4	256	–	6	13	1909	57	3124	2460	–	53	11
Wuluh River 1															
0–0.05	6.4	180	236	36	1733	7.3	2.5	93	2.2	41	1358	1835	68	80	–
0.5–0.1	7.1	116	220	23	1115	5.1	2.6	96	2.4	40	1292	1669	52	59	–
0.1–0.3	7.4	112	197	4.5	331	1.7	2.3	107	2.4	45	1517	2181	18	12	–
0.3–0.5	8.5	142	180	1.8	173	1.0	2.3	86	2.7	40	1310	1723	2.1	20	–
0.5–0.75	9.2	726	204	5.1	6218	30.4	2.1	82	2.1	39	1233	1829	6.6	13	–
Bedrock	–	–	1.8	0.05	326	–	4.7	8	2455	42.5	860	1111	–	24	13

TABLE 9

Soil parameter	Unit	Cuba	Brazil*	New Caledonia	Indonesia	Indonesia	Indonesia	Philippines	Malaysia
					(Sulawesi)	(Sulawesi)	(Mt Piapi)	Mt Giting–Giting	(Mt Kinabalu)
Altitude	m asl	–	750–1100	–	–	200–300	60–500	325–1540	400–2900
pH	–	–	–	4.4–6.9	5.3–6.3	5.8–6.1	6.1–6.4	4.3–5.5	3.8–9.7
CEC	cmol ⁽⁺⁾ kg ⁻¹	–	0.3–82.9	1.2–34	–	43–67 ⁶	15–44	–	0.03–128 ¹
Mg:Ca	–	–	8.3–24	0.8–23	0.9–5.7	0.6–2.1 ⁶	1.6–32	0.3–2.9 ²	0.1–136 ¹
Ca (exch.)	cmol ⁽⁺⁾ kg ⁻¹	–	0.015–1.9	0.01–1.8	4.6–13.3	0.6–0.1 ⁶	0.9–16	0.5–3.4 ²	0.003–35 ¹
Ca (pseudo-total)	µg g ⁻¹	4800	0–13500	–	–	–	–	–	7.7–39300
Mg (exch.)	cmol ⁽⁺⁾ kg ⁻¹	–	0.004–1.9	0.2–38.5	11.1–26.2	0.52–1.18 ⁶	13.9–27.3	0.75–3.64 ²	0.02–76 ¹
Mg (pseudo-total)	mg/g	–	12–154	–	–	–	–	–	0.27–235
K (exch.)	cmol ⁽⁺⁾ kg ⁻¹	–	–	0.02–0.2	0.05–0.5	0.03–0.10 ⁶	0.19–0.38	0.04–0.41 ²	0.002–0.79 ¹
K (pseudo-total)	µg g ⁻¹	740	–	–	–	5164–6260 ⁴	–	–	0.1–1056
P (pseudo-total)	µg g ⁻¹	1724	< 100	393–509	–	95–237 ⁴	–	–	4.4–585
P (extract.)	µg g ⁻¹	–	–	140–310	–	1.7–3.8 ⁷	0.94–6.8 ³	0.41–2.07 ³	0.1–32 ⁹
Fe (pseudo-total)	mg g ⁻¹	196	154–466	–	–	132–293	–	–	21–535
Ni (pseudo-total)	µg g ⁻¹	4674	7744–18520	1300–10400	825–4050	3730–7051 ⁴	–	–	17–9308
Ni (extract.)	µg g ⁻¹	–	0–1232	0.2–66	–	6.0–7.5 ⁶	8.5–37 ⁵	1–24 ⁵	0.17–442 ⁸
Cr (pseudo-total)	mg g ⁻¹	3.8	11200–46800	6.3–56	1.0–9.9	9.5–17 ⁴	–	–	121–21710
Cr (extract.)	µg g ⁻¹	–	80–980	0.6–8.1	1	–	–	–	< 0.1–13 ⁸
Co (pseudo-total)	µg g ⁻¹	381	413–799	230–1300	–	57–337 ⁴	–	–	0.5–1524
Co (extract.)	µg g ⁻¹	–	–	76–116 ⁸	–	–	–	–	0.04–96 ⁸
References		Reeves et al., 1999	Raous et al. 2013	Jaffré, 1980	Parry, 1985	Tjoa, 2011	Proctor et al., 1994	Proctor et al., 1998	This research

NOTES: ¹ CEC and exchangeable cations with silver-thiourea, ² CEC and exchangeable cations with ammonium acetate, ³ Olsen-P extract (NaHCO₃), ⁴ Soil digestion with HNO₃/HCl, ⁵ Ammonium acetate extract, ⁶ Acetic acid extract/digestion, ⁷ Bray's extract, ⁸ DTPA-extract, ⁹ Mehlich-3 extract. *Total concentrations instead of pseudo-total.